

# Canonical morphometry *versus* statistical treatment of outlines through Fourier shape analysis: an empirical comparison

Francesco Brusoni\* & Daniela Basso# (✉)

\* Via S. Maria del Sole 10,  
26900 Lodi, Italy,  
f.brusoni@katamail.com

# Dip.to di Sc.  
Geologiche  
e Geotecnologie,  
Università degli Studi  
di Milano-Bicocca,  
Piazza della Scienza 4,  
20126 Milano, Italy,  
daniela.basso@unimib.it,  
(✉) Corresponding  
Author

## Abstract

The analysis of outlines is considered a powerful tool for morphometric studies, since the absence of assumptions on characters to be selected and measured reduces subjectivity. Fourier shape analysis converts each digitalized outline into a suite of numerical descriptors (the Fourier coefficients) that describe curves. The coefficients are the input to multivariate statistical analyses, that elaborates a numerical comparison of shapes. A friendly, easily accessible and practical method for a statistical approach to shape analysis and the sensitivity of both Elliptic Fourier Analysis and Fast Fourier Transform have been tested here on a set of *Goodallia triangularis* shells. Shape analysis results to be faster and more reliable than canonical morphometry. In the comparison of the Principal Component Analyses based on the two different Fourier transformations, Fast Fourier Transform produces the sharpest separation of the shell outlines into clusters while Elliptic Fourier Analysis results are comparably less clear. Both techniques easily separate the two forms of *Goodallia triangularis*.

## Riassunto

La descrizione quantitativa delle forme biologiche viene tradizionalmente affidata alla morfometria. Nella routine, la tecnica morfometrica viene tuttavia applicata a un limitato numero di caratteri misurabili, scelti in modo più o meno arbitrario, riconducendo quindi la variabilità registrata a pochi parametri. Molte caratteristiche morfologiche vengono tradizionalmente descritte in modo qualitativo (ad esempio la convessità della spira nei gasteropodi), senza quindi assegnare alcun parametro matematico di misura che possa successivamente consentire un confronto su base statistica-quantitativa.

Per evitare che la scelta arbitraria di alcuni caratteri rispetto ad altri influenzi il risultato dello studio morfologico-comparativo sarebbe necessario considerare la totalità dei caratteri misurabili. Il tentativo di avvicinarsi a tale situazione ideale, evitando una eccessiva semplificazione, richiede tuttavia un enorme dispendio di tempo. A questo si aggiunge la percentuale di errore dovuta alla misurazione manuale e l'aumento delle difficoltà quando le dimensioni degli oggetti di studio sono molto ridotte.

La trasformazione del profilo di una struttura biologica in una serie di parametri matematici (*shape analysis*) in luogo delle misure morfometriche tradizionali, consente di ridurre notevolmente la componente soggettiva e di sostituire o affiancare, in molti casi, il metodo tradizionale di misurazione. Nella *shape analysis*, la forma è ricondotta ad un'unica computazione, che, a sua volta, riassume in sé tutte le misure quali altezza, larghezza, curvature ed angoli. Si ottiene quindi quella che si potrebbe definire la "formula geometrica" che descrive l'esemplare nella sua globalità, che può essere convenientemente trattata in analisi statistiche successive.

Il metodo è applicabile a strutture di qualunque genere, tenendo sempre presente la necessità di operare confronti tra punti tra loro omologhi. Allo stato attuale della tecnologia comunemente disponibile, le conchiglie dei molluschi sembrano prestarsi meglio a questo tipo di analisi, in quanto più facilmente riconducibili ad un profilo bi-dimensionale di punti tra loro omologhi.

In questo lavoro si confrontano i risultati della morfometria tradizionale (peso, lunghezza, altezza e spessore di ciascuna valva) e di alcuni metodi facilmente accessibili di *shape analysis*, basati sull'analisi di Fourier, applicati ad uno stesso gruppo di 39 valve destre di *Goodallia triangularis*.

Sono stati utilizzati softwares differenti per trasformare le immagini digitali degli oggetti in parametri matematici. Una volta acquisita l'esperienza sufficiente, il tempo necessario per passare dall'immagine digitalizzata alla serie di Fourier pronta per l'elaborazione statistica è di pochi minuti per ciascuna valva. Per passare dall'acquisizione delle immagini digitali al risultato finale dell'analisi statistica multivariata sono state impiegate complessivamente poche ore.

Il dendrogramma e la PCA eseguite sui profili delle 39 valve di *G. triangularis* mostrano una separazione in due gruppi, corrispondenti alle due forme di *Goodallia triangularis*: una con profilo tendenzialmente triangolare e una di forma più allungata, in accordo con precedenti conclusioni di altri autori.

Nel caso considerato, la *shape analysis* è risultata notevolmente più rapida e ha prodotto risultati più attendibili e di più semplice interpretazione rispetto ai metodi morfometrici tradizionali.

## Key words

Fourier shape analysis, bivalve, outline, methods.

## Introduction

Identification of shelled species based on external morphology is still the basis of all subsequent elaborations

in many diverse disciplines such as palaeontology, biogeography, ecology and palaeoecology and their applications. Biological structures and shapes are often very complex and their morphometric description triggers at

least four major problems: 1) the inadequacy of the use of a limited number of linear variables to describe a three-dimensional object; 2) the time-consuming job required when trying to use as many linear variables as possible; 3) the arbitrary choice of characters to be measured, that commonly leads to difficulties in comparing results from different researchers; 4) in small-sized, the difficulty to achieve a quantitative description of their morphology and the incidence of operator precision in the accuracy of measurements.

Recent advances in information technology made available some user-friendly softwares for image manipulation and multivariate statistical analysis. In some instances these softwares are freely accessible from the web and possess a wide pool of potential users.

The opportunity to use low-cost and friendly technologies with the aim to reduce subjectivity (in morphological data acquisition) and loss of time (for sample and data manipulation), has been approached since the late eighties. It has been shown that Fourier shape analysis (FSA) is particularly useful for numerical description of diverse organisms or biological structures such as coccoliths (Garratt & Swan, 1997), leaves (White *et al.*, 1988), foraminifers (Healy-Williams, 1984; Belyea & Thunell, 1984), bivalves (Ferson *et al.*, 1985; Crampton, 1996; Crampton & Maxwell, 2000), trilobites (Foote, 1989; Cronier *et al.*, 1998), ostracodes (Burke *et al.*, 1987; Foster & Kaesler, 1988), blastoid echinoderms (Waters, 1977), bryozoans (Anstey & Delmet, 1973) and fish ooliths (Gauldie & Crampton, 2002; Lombarte *et al.*, 2006).

FSA takes an outline contour, described as a polygon of digitized XY-coordinates, and decomposes it into a spectrum of harmonically related trigonometric curves. Principles of FSA have been developed into different transformations. In particular, the Elliptic Fourier Analysis (EFA; Kuhl and Giardina, 1982) and the Fast Fourier Transform (FFT) have been used within DOS-based softwares devoted to shape analysis of fossils (Crampton, 1995).

The analysis of outlines is considered a powerful tool for morphometric studies, especially when homologous structures are lacking and consequently, landmark-based measurements do not apply (Harper, 1999). Fourier shape analysis converts each digitized outline into a suite of numerical descriptors (the Fourier coefficients) that describe curves (Crampton & Maxwell, 2000). The coefficients are the input to multivariate statistical analyses, that elaborates a numerical comparison of shapes. Haines & Crampton (2000) observed that EFA yields a relatively large number of Fourier coefficients that are not computationally independent of each other. This redundancy would hamper and compromise the statistical multivariate analysis of coefficients. To overcome this problem, it has been proposed another method of FSA called Fast Fourier Transform (FFT; Crampton, 1995). The aim of this paper is to suggest a friendly, easily accessible and practical method for a statistical approach to shape analysis and to explore the sensitivity of both EFA and FFT by comparison with results of traditional morphometrics.

## Material e methods

Shell size is here intended as a proxy for age, even though the direct correlation between size and age is not equivalent for all specimens (Jones, 1988).

Digital images of 39 right valves of the small bivalve *Goodallia triangularis* (Montagu, 1803) were obtained from a microscope Olympus BX 50 equipped with a digital camera Camedia C 2000z and software Camedia DP-soft. The digital pictures have been transformed into simple shell outlines (profiles), and then into a series of mathematical parameters to be analysed by multivariate statistics (Fig. 1).

Presently, the entire procedure requires four different softwares. A common graphic software to extract the profile; a software for image manipulation and photo touch that can produce the co-ordinates of each pixel of the profile; a common work-sheet to store the co-ordinates and their Fourier transform; "PAST", a free software for statistical analyses in biology and palaeontology (Hammer *et al.*, 2005) allowing to standardize data and to perform multivariate statistical analysis of profiles (similarity matrix, dendrogram and Principal Component Analysis). FFT coefficients have been obtained with the programs Hmatch and Hangle (Crampton & Haines, 1996) and subsequently elaborated with PAST in order to perform the analysis of similarity and the PCA ordination.

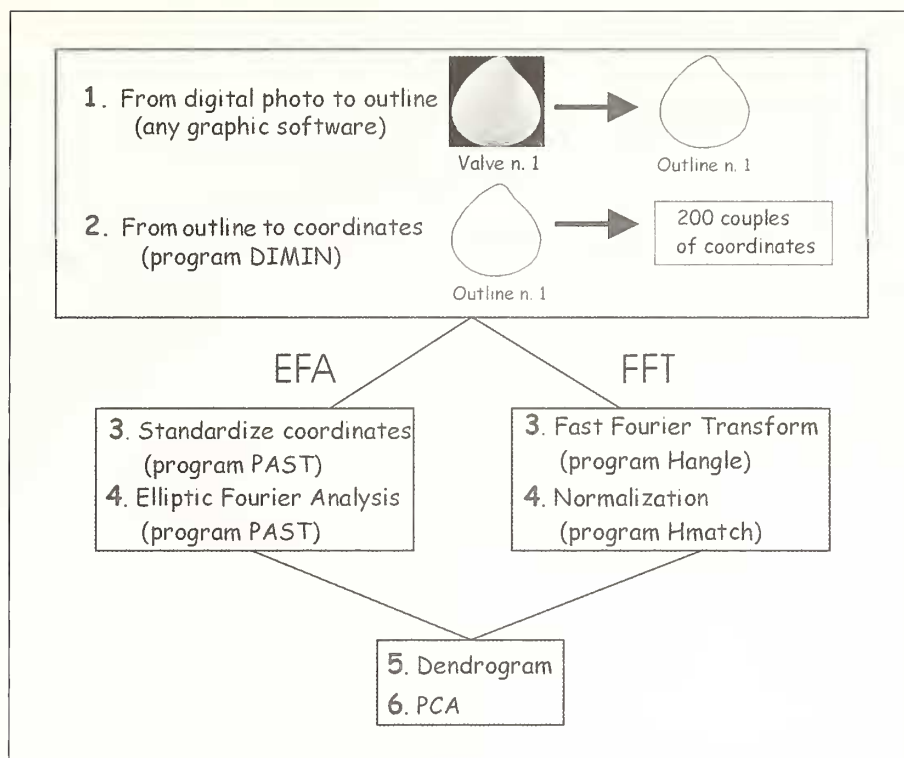
The valves have been randomly extracted from the 250 right valves on which a morphometric analysis based on weight (as a proxy of shell thickness), length, height and width (as synthetic descriptors of shape) of each valve was already performed (Basso, 1992). This approach allows the comparison of the results obtained with the traditional method and with the digital-profiles method. Procedural details are listed in appendix.

## Results

The multivariate statistical analysis of outlines of 39 *G. triangularis* right valves produced graphic results (dendrogram and PCA scatter plots, Figs. 2-5) in which each point represents one right valve profile. The statistical analysis produced different results for EFA- and FFT-based shape analysis. Some representative outlines are reported over the corresponding number in the PCA plot.

### Elliptic Fourier Shape Analysis

The dendrogram (Euclidean distance, paired groups, Fig. 2) and the PCA (Fig. 3) based on the 39 profiles of *G. triangularis* right valves show three clusters (A to C). Cluster A is made of ventrally rounded valves (*G. triangularis* forma *subtrigona*), cluster B contains valves with more triangular shape (*G. triangularis* forma *typica*) (Fig. 2). Cluster C contains valves with intermediate shapes and the shell outlines at its border could be included in the first and second clusters. In the third cluster, outlines no. 37 and 5 correspond to intermediate shapes. Results of PCA (Fig. 3) show that the first two components represents about 91% of the total variability.



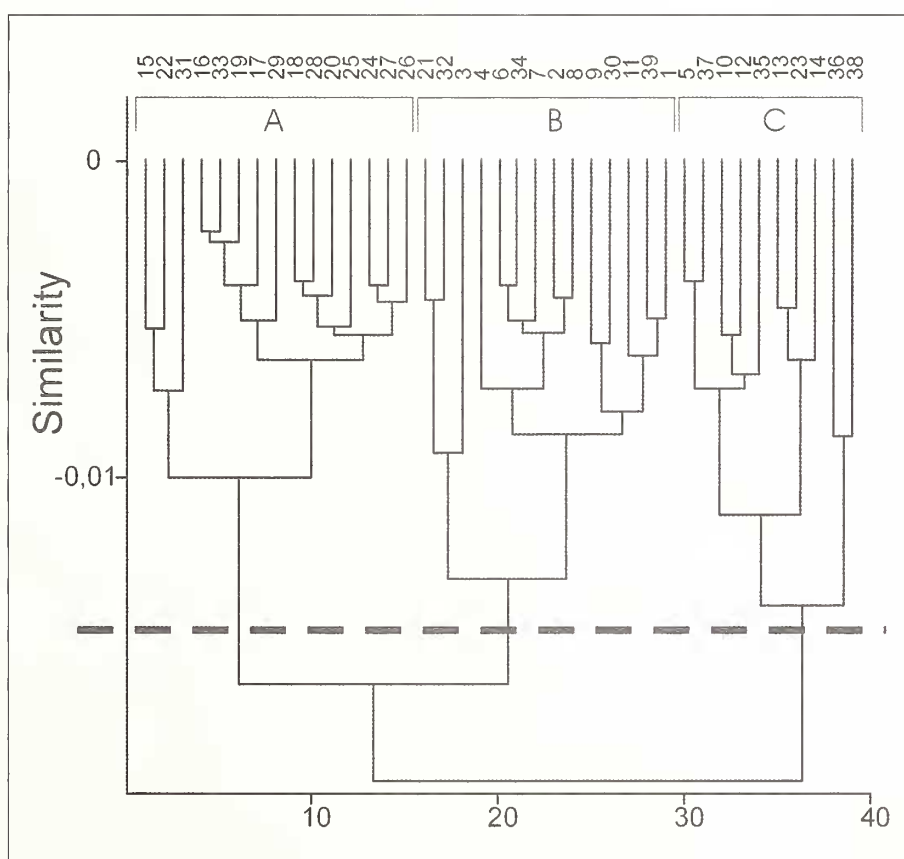
**Fig. 1.** Schematic procedure to perform multivariate statistical analysis of shell outlines. Details in the Appendix.

**Fig. 1.** Schema della procedura per eseguire un'analisi statistica multivariata su profili di conchiglie. Dettagli in Appendice.

### Fast Fourier Transform

The dendrogram based on coefficients produced by FFT (Euclidean similarity, paired groups, **Fig. 4**) shows only 2 clusters (A and B), represented also in the PCA scatter plot (**Fig. 5**). Cluster A includes *G. triangularis* form *subtrigona* and cluster B encompasses specimens of *G. triangularis* form *typica*. The shells with the maximum length/height

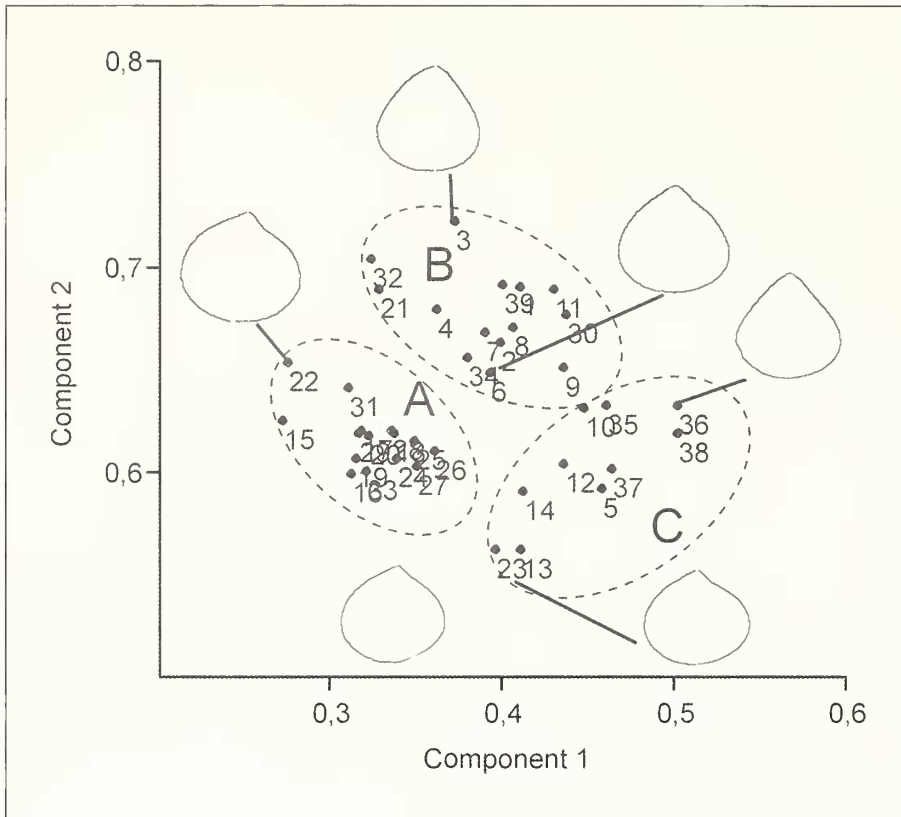
ratio are concentrated between values of 0.02 and 0.01 of the first component and between 0 and 0.04 of the second component. The intermediate shell outlines that were plotted in cluster C (EFA plot) are here splitted into clusters A and B. In particular, outlines no. 5, 12 and 37 are assigned to cluster B, close to the boundary with cluster A. As a result, FFT produces a sharp separation of the outlines into clusters.



**Fig. 2.** Dendrogram produced by hierarchical clustering of trigonometric coefficients (corresponding to the outlines) obtained with EFA. Clusters A to C are obtained at the  $-0,015$  level of Euclidean distance. Clustering calculated on unweighted pair-group average (UPGMA).

**Fig. 2.** Dendrogramma prodotto dal clustering gerarchico agglomerativo dei coefficienti trigonometrici (corrispondenti ai profili) ottenuti con l'Analisi Ellittica di Fourier (EFA). I gruppi da A a C si separano alla distanza euclidea =  $-0,015$ . Il clustering è calcolato sul legame medio (UPGMA).





**Fig. 3.** PCA scatter plot based on the same coefficients (EFA) and Euclidean distance of Fig. 2. The A to C clusters are indicated.

**Fig. 3.** Grafico PCA basato sugli stessi coefficienti (EFA) e distanze euclidee di Fig. 2. Sono indicati i gruppi da A a C.

## Discussion

In order to study the morphometric variability of *Goodallia triangularis* occurring in a Mediterranean shell assemblage (= thanatocoenosis), Basso (1992) faced the difficulty to measure and deal with valves that rarely exceeded 3.3 mm in length. It was required a time-consuming job and the use of high-precision calibres and balance. Subsequently, bivariate and multivariate statistical analyses of the measured variables allowed the recognition of two ecomorphotypes of *G. triangularis*, one more triangular, representing the Atlantic, cold-water form and now occurring in the relict sediment of the Mediterranean shelf-break; the other more elongate, which is the Mediterranean living form (form *subtrigona*) (Fig. 6). These conclusions were later confirmed by Giribet & Peñas (1999) in the framework of the revision of the genus *Goodallia*. The occurrence of intermediate specimens, as observed by Basso (1992), prevents the separation of these eco-morphotypes into different species. In the same paper (Basso, 1992), most of these intermediate specimens, interpreted as juveniles on the basis of their very small size, were positioned at the left end of the PCA scatter plot (Basso, 1992, Fig. 6). The largest specimens were spread along the right end of the PCA plot, with the longest and relatively light valves at the bottom right (form *subtrigona*), and the highest, relatively heavy valves at the top right of the plot (form *typica*; Basso, 1992, Fig. 6).

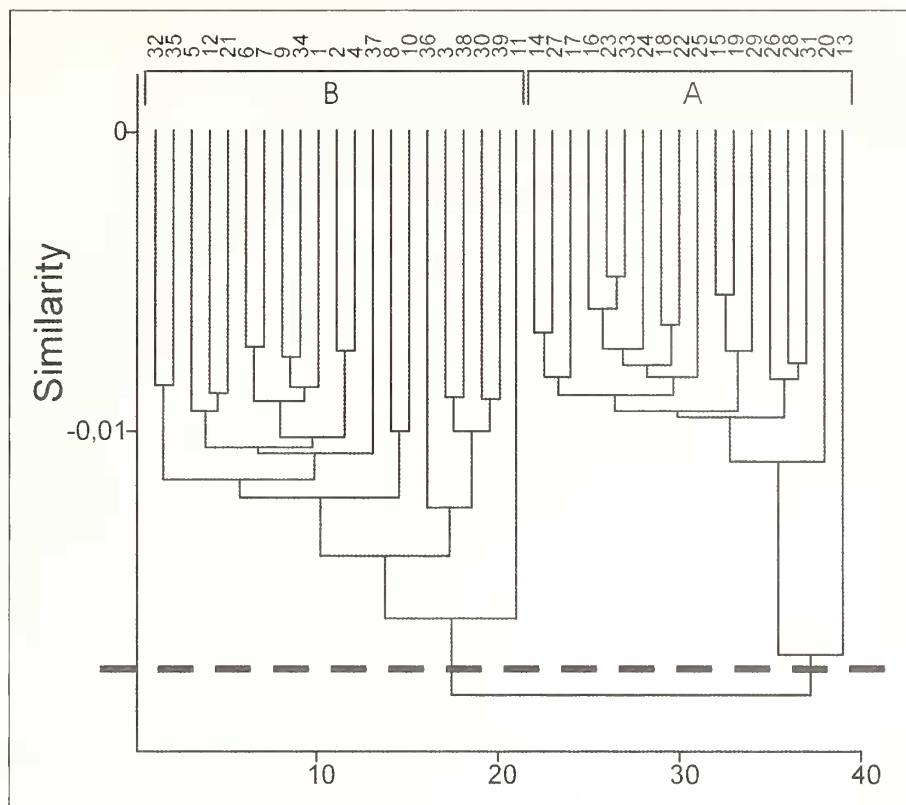
The complete outline of the shells of the two subspecies of *Goodallia triangularis* summarizes the general shape, the slope of the margins and the roundness, and the more or less equilaterality of the bivalve on the basis of the position of the umbo (orthocline in the subspecies

*typica*, prosocline in the *subtrigona*). Unlike "traditional" morphometrics, shape analysis considers only profiles and disregards dimensions. Therefore, unlike Basso (1992) our results show juvenile shells within all three clusters of EFA-based dendrogram, to indicate a possible early divergence in shell morphology.

When a convenient number of specimens is available, it is possible to study the reciprocal position of the "cloud" of points in the PCA plot, along possible gradients of shape variability.

It is of a paramount importance to verify that the samples are photographed with exactly the same position. Although PAST contains a standardization procedure allowing to deal with some variability in sample orientation, it is better to homogenize the orientation in order to avoid confusion or subjective bias in the subsequent phases. Moreover, it must be considered that possible displacements of a bivalve shell are in one plane only, and that is quite easily managed with PAST standardization. Major problems are expected to arise from gastropod shell orientation, since rotation along the long axis of the shell or tilting will result in a different profile on the plane, and thus the same shell variably oriented will be recognized as a different object. This kind of biased image acquisition cannot be solved by PAST standardization (Hammer *et al.*, 2005).

Most difficulties arise in establishing an homology between points of profiles; points must be phylogenetically homologous in order to perform a meaningful statistical analysis. (Bookstein *et al.*, 1982; Read & Lestrel, 1986; Temple, 1992). In many cases it is possible to identify homologous points in a biological specimen. These points are taken as landmarks in traditional morphometry. Thousands of literature examples cover very di-

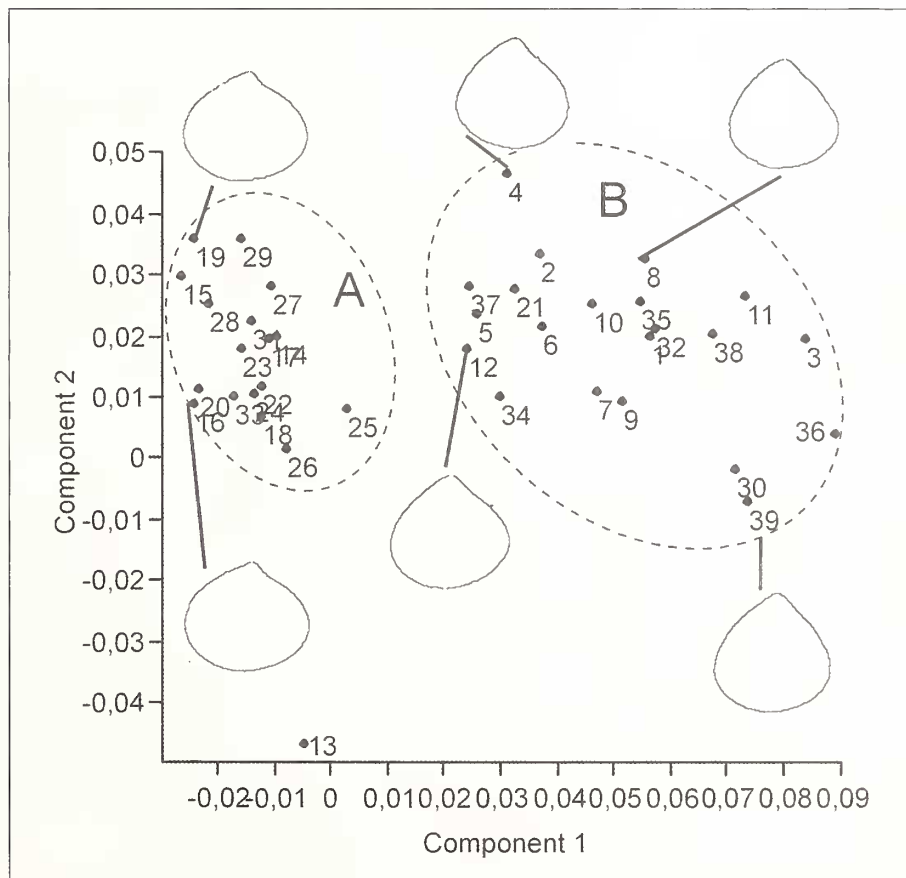


**Fig. 4.** Dendrogram produced by hierarchical clustering of trigonometric coefficients (corresponding to the outlines) obtained with FFT. Clusters A and B are obtained at the  $-0,017$  level of Euclidean distance. Clustering calculated on unweighted pair-group average (UPGMA).

**Fig. 4.** Dendrogramma prodotto dal clustering gerarchico agglomerativo dei coefficienti trigonometrici (corrispondenti ai profili) ottenuti con Trasformata Veloce di Fourier (FFT). I gruppi A e B si separano alla distanza euclidea di  $-0,017$ . Il clustering è calcolato sul legame medio (UPGMA).

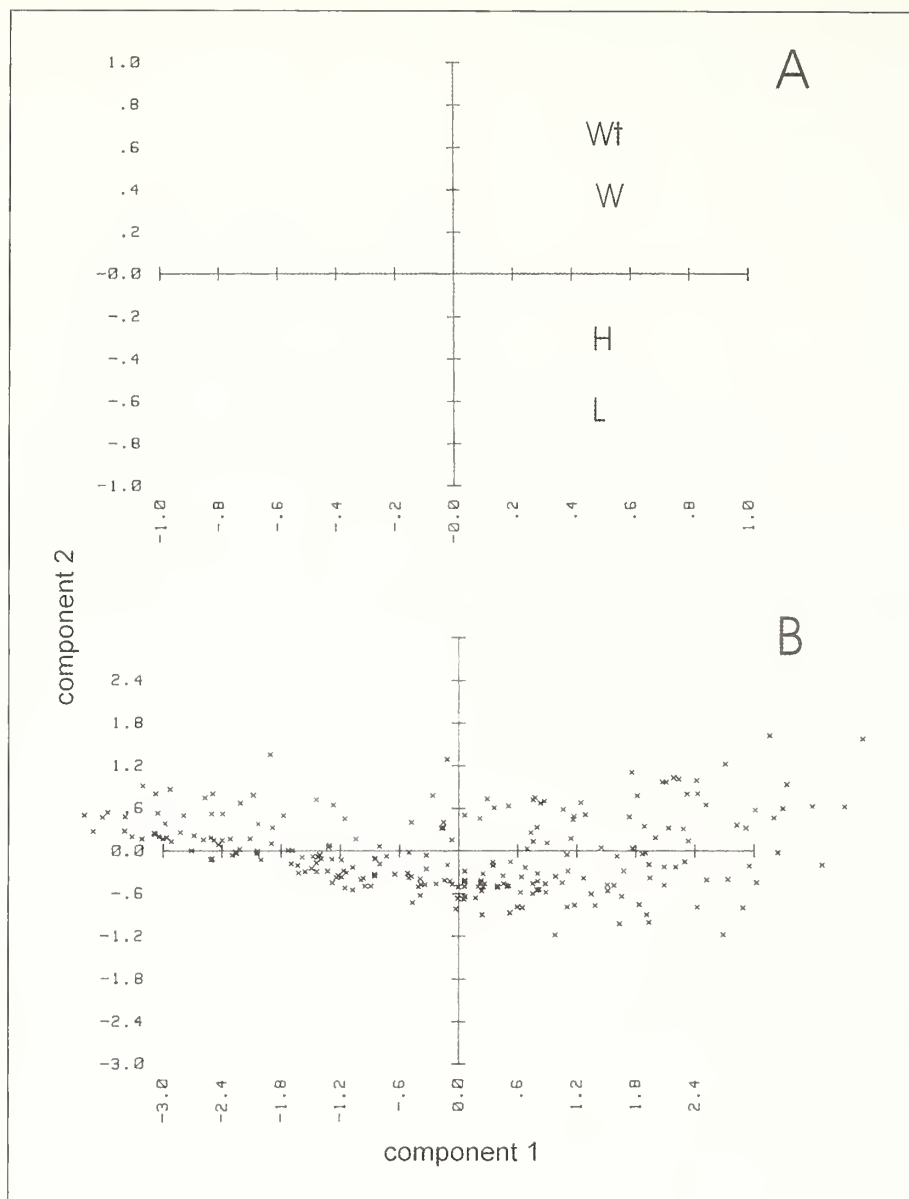
verse subjects such as trilobites, molluscan shells or the biometry of human skull (for example: Hughes & Chapman, 1995; Lacroce & Repetto, 2004). In other instances these points that are easily identified from a biological point of view, are difficult to locate with precision in the practice. This can be the case of the bivalve umbo that corresponds to a small area on the shell ra-

ther than a precise point (Crampton, 1995; Crampton & Haines, 1996). This problem represent a possible source of uncertainty in manual measurements, and is negligible only for large-sized specimens. Similarly, it is difficult to locate homologous points on the spire of gastropods, with the exception of the apex (protoconch). The use of a complete outline, as in Fourier shape analysis,



**Fig. 5.** PCA scatter plot based on the same coefficients (FFT) and Euclidean distance of Fig. 4. The A and B clusters are indicated (from Basso, 1992).

**Fig. 5.** Grafico PCA basato sugli stessi coefficienti (FFT) e distanze eucldee della Fig. 4. Sono indicati i gruppi A e B (da Basso, 1992).



**Fig. 6.** A. Principal component analysis for L = length; H = height; W = width; Wt = weight. B. component scores plot (from Basso, 1992).

**Fig. 6.** A. Analisi dei componenti principali (PCA) per L = lunghezza; H = altezza; W = spessore; Wt = peso. B. Grafico dei component scores (da Basso, 1992).

corresponds to the use of all homologous points at the same time, therefore the identification of selected landmarks is no more necessary (Foote, 1989). However, all specimen outlines must be obtained with the same specimen orientation, in order to allow comparison among series of homologous points.

Haines & Crampton (2000) observed that EFA yields a relatively large number of Fourier coefficients that are not computationally independent of each other. This redundancy would hamper and compromise the statistical multivariate analysis of coefficients. Actually, FFT of our *Goodallia* outlines produces the sharpest separation of the shells into clusters, which is an obvious advantage for interpretation. EFA results are comparably less clear. Interestingly, the same outlines (15 and 36) are at the opposite ends along component 1 in both PCA, while outlines 23 and 3, that are opposite along component 2 in EFA (Fig. 3), are also split by component 1 in FFT (Fig. 5).

The procedure used here is much faster and simple in comparison with traditional morphometrics and allows an easier graphic interpretation of results. Despite the use of several different softwares, the entire procedure from digital photographs to dendrogram and PCA plots

required few hours (Fig. 1). With some practice, only few minutes are necessary to produce the Fourier series from the digital picture.

## Conclusions

This paper is aimed to compare the performance of traditional morphometrics and of FSA in the description of small bivalves. In agreement with Davoli (1982), the best practice of a morphologic-comparative study should be the use of observations and measurements of all morphological variables, avoiding the use of few, arbitrarily chosen characters of classification. In the case of *Goodallia*, the very small size and the fragility of shells prevent the collection of further linear measurements in addition to shell length, height and width considered by Basso (1992). Moreover, some morphologic features are traditionally defined in a qualitative way (such as the symmetry of the bivalve shell and its roundness), preventing their quantification, objective definition and statistical treatment.

The first advantage of FSA is the absence of assumptions on characters to be selected and measured. The transformation of the outline of a biological structure



into a suite of mathematical parameters reduces subjectivity since outlines are the synthesis of many measurements (height, length, width, slopes, convexity, etc.). It can be argued that some features cannot be detected by FSA of outer side of bivalve shells, such as internal structures, shell thickness or ornamentations. However, most internal features of bivalves correspond to major supraspecific diagnostic characters, such as the type of pallial line (integer or with a sinus) and the hinge structure, that are efficiently and quite rapidly described in the traditional qualitative approach. Moreover, thick ornamentation such coarse ridges and costae, spines etc. are expected to be detectable along the outline.

Multivariate statistical elaboration had analogous bearing in respect to the traditional morphometry, leading to an easy separation of the two forms of *Goodallia* with a much faster and less subjective procedure. The same results, obtained with the canonical morphometry based on linear measurements (Basso, 1992), required electronic instruments for precision mechanics and a time-consuming specimen manipulation. The second advantage of FSA is the objectiveness and the rapidity of data acquisition.

In the comparison of the PCA results based on the two different Fourier transformations, FFT produces the sharpest separation of the outlines into clusters while EFA results are comparably less clear (Figs 2- 3).

At the present state of the art, FSA is not expected to substitute all canonical morphometric methods. A critical point remains the choice of topics that can be successfully afforded through the comparison of bi-dimensional profiles of homologous points, as most bivalves are. Gastropods could be eligible for FSA, provided that a constant orientation of the specimens is ensured. Among bivalves, the analysis of similarity among different species of the same genus or among infraspecific taxa appears particularly promising.

The method described in this paper involves the use of different softwares. Work is in progress to merge and integrate them into one single software that would be a step forwards the divulgation of such a powerful technique.

## Appendix

### Procedure:

#### 1) Digital photographs

Specimens must be complete and broken margins must be avoided, since they will be interpreted by FSA as a dramatic change of outline. The color of the specimen background should be selected to contrast the shell outline and enhance separation while working at pixel level.

#### 2) Obtaining outlines

All digital pictures to be dealt with must have standard size (pixels) in order to obtain black outlines, composed of the same number of points, on a white background (colours can be inverted). This condition must be satisfied when entering the PAST procedures for similarity analysis. Common graphic softwares can be used to obtain the simple shell outlines and "clean" them from possible "noise" pixel generated by dust, shadows etc.

#### 3) Transforming the outline graphic file into a suite of co-ordinates (X, Y)

Most common softwares will "read" the outline the occidental way: from left to right, from top to bottom, as a written text. On the contrary, the outline transformation into co-ordinates requires to read it counterclockwise, each pixel only once. Therefore it is necessary to divide each valve profile into half (right and left) the will be dealt with separately. Successively the two halves will be converted in ASCII (.dat) file containing the points co-ordinates.

The ASCII file contains the description of the profile given by the co-ordinates of all the composing points. Opening the electronic sheet of each half profile we will find three columns: the first for abscissas, the second for ordinates, the third for the RGB colour of each point. Using filters it is possible to separate the profile points from the background simply selecting the colour (black points = RGB 0). After this stage a new file should be created containing only the two columns of co-ordinates.

The same procedure is repeated for the other half profile that must be put upside down, in order to allow joining the first half reading the whole profile counter clockwise. This way the table will show the co-ordinates of points of the profile starting from the uppermost point of the left half-profile, down to the lowermost point of the same left half-profile, up in a counter clockwise sense from the lowermost point of the right half-profile to the uppermost point of the same right half-profile.

All couples of co-ordinates (the first for abscissas, the second for ordinates) pertaining to all outlines should be saved in the same file.

Example:

X1a	Y1a	X1b	Y1b	.....	where each letter <i>a, b, ...</i>
X2a	Y2a	X2b	Y2b		identifies an outline
X3a	Y3a	X3b	Y3b		
.....		.....			

#### 4) Transformation of co-ordinates into coefficients

Two different pathways are followed depending on the selected type of Fourier transform: Elliptic Fourier Analysis or Fast Fourier Transform.

Elliptic Fourier Analysis (EFA)

PAST programs

The co-ordinates file is copied into PAST (Hammer *et al.*, 2005). It is now necessary to transpose the matrix of co-ordinates on a line, alternating abscissas and ordinates:

Example:

X1a	Y1a	X2a	Y2a	X3a	Y3a	.....
X1b	Y1b	X2b	Y2b	X3b	Y3b	.....

This can be obtained with the PAST function "GROUPED COLUMNS TO MULTIVAR", (EDIT menu) indicating two dimensions. Then the transpose function can apply.

In order to standardize profiles in size and rotation on the plane, it is necessary to use the PAST function *PROCRUSTES*. This function can be lengthy but is necessary to give profiles the same orientation. Now profiles are converted

with the function *ELLIPTIC FOURIER SHAPE ANALYSIS* in a sequence of trigonometric coefficients (Ferson *et al.*, 1985).

Fast Fourier Transform (FFT)

HANGLE, HMATCH programs

The co-ordinates file is the input for the program *HANGLE* (Crampton & Haines, 1996) that output the Fourier coefficients. Successively, the *HMATCH* program normalizes the Fourier coefficients of each outline for orientation and starting position of the trace.

## 5) Multivariate statistical analysis

PAST can also be used for classification and ordination of coefficients obtained with EFA or FFT (cluster analysis and Principal Components Analysis = PCA). In this paper we used Euclidean distance and unweighted pair-group average (UPGMA). PAST has other functions devoted to improve the interpretation of PCA ordination, such as the *MINIMUM SPANNING TREE* or the 3D option for the multidimensional disposition and relationship of points in the plot.

## Acknowledgements

We thank Francesco Livraghi for his assistance on informatics engineering. Sincere thanks are due to J.S. Crampton and O. Hammer for their hints on software application. We are grateful to Elio Robba for his constructive suggestions. Thanks are due to M. Chiantore and an anonymous referee for the revision of the manuscript.

## References

- ANSTEY R.L. & DELMET D.A., 1973. Fourier analysis of zoecial shapes in fossil tubular bryozoans. *Bulletin of the Geological Society of America*, **84**: 1753-1764.
- BASSO D., 1992. Shell variability in *Goodallia* (*Goodallia*) *triangularis* (Montagu, 1803), (Bivalvia Crassatelloidea). *Lavori S.I.M.*, **24**: 17-30.
- BELYEA P.R. & THUNELL R.C., 1984. Fourier shape analysis and planktonic foraminiferal evolution: the *Neogloboquadrina-Pulleniatina* lineages. *Journal of Paleontology*, **58**: 1026-1040.
- BOOKSTEIN F.L., STRAUSS R.E., HUMPHRIES J.M., CHERNOFF B., ELDER R.L. & SMITH G.R., 1982. A comment upon the use of Fourier methods in systematics. *Systematic Zoology*, **31**: 85-92.
- BURKE C.D., FULL W.E. & GERNANT R.E., 1987. Recognition of fossil freshwater ostracodes: Fourier shape analysis. *Lethaia*, **20**: 307-314.
- CRAMPTON J.S., 1995. Elliptic Fourier shape analysis of fossil bivalves: some practical considerations. *Lethaia*, **28**: 179-186.
- CRAMPTON J.S. & HAINES A.J., 1996. *User's manual for programs Hangle, Hmatch and Hcurve for the Fourier shape analysis of two-dimensional outlines*. Institute of Geological & Nuclear Sciences, Science Report 96/37, 28 pp.
- CRAMPTON J.S. & MAXWELL P.A., 2000. Size: all it's shaped up to be? Evolution of shape through the lifespan of the Cenozoic bivalve *Spissatella* (Crassatellidae). In HARPER, E.M., TAYLOR, J.D. & CRAME, J.A. (eds.). *The evolutionary biology of the Bivalvia*. Geol. Soc., London, Sp. Publ., **177**: 399-423.
- CRONIER C., RENAUD S., FEIST R. & AUFRAY J.-C., 1998. Ontogeny of *Trimerocephalus lelievrei* (Trilobita, Phacopida), a representative of the Late Devonian phacopine pedomorphocline: a morphometric approach. *Paleobiology*, **24**: 359-370.
- DAVOLI F., 1982. Cancellariidae (Gastropoda). In: E. MONTANARO GALLITELLI (ed.) *Studi monografici sulla malacologia miocenica modenese. Parte I – I molluschi tortoniani di Montegibbio*. *Paleontographia Italica*, **72**: 5-73.
- FERSON S., ROHLF E.J. & KOEHN R.K., 1985. Measuring shape variation of two-dimensional outlines. *Systematic zoology*, **34**: 59-68.
- FOOTE M., 1989. Perimeter-based Fourier analysis: a new morphometric method applied to the trilobite cranium. *Journal of paleontology*, **63**: 880-885.
- FOSTER D.W. & KAESLER R.L., 1988. Shape analysis. Ideas from the Ostracoda. 53-69. In: MCKINNEY M.L. (ed.) *Heterochrony in evolution: a multidisciplinary approach*. *Topics in Geobiology*, **7**. Plenum Press, New York, 348 pp.
- GARRATT J.A. & SWAN A.R.H., 1997. Fourier transforms of image-derived data: application to Albian coccoliths. *Micro-paleontology*, **43**: 303-317.
- GAULDIE R.W. & CRAMPTON J.S., 2002. An eco-morphological explanation of individual variability in the shape of the fish otolith: comparison of the otolith of *Hoplostethus atlanticus* with other species by depth. *Journal of Fish Biology*, **60**: 1204-1221.
- GIRIBET G. & PEÑAS, 1999. Revision of the genus *Goodallia* (Bivalvia: Astartidae) with the description of two new species. *Journal of Molluscan Studies*, **65**: 251-265.
- HAINES J. & CRAMPTON J.S., 2000. Improvements to the method of Fourier shape analysis as applied in Morphometric studies. *Palaeontology* **43**: 765-783.
- HAMMER O., HARPER D.A.T. & RYAN P.D., 2005. PAST – Palaeontological statistics, ver. 1.33. On line at <http://folk.uio.no/ohammer/past>
- HARPER, 1999. *Numerical Palaeobiology - Computer-based modeling and analysis of fossils and their distribution*. Chichester, England, John Wiley & Sons Ltd., 478 pp.
- HEALY-WILLIAMS D.F., 1983. Fourier shape analysis of *Globorotalia truncatulinoides* from late Quaternary sediments in the southern Indian Ocean. *Marine Micropaleontology*, **8**: 1-15.
- HUGHES N.C. & CHAPMAN R.E., 1995. Growth and variation in the Silurian proetide trilobite *Aulacopleura konincki* and its implications for trilobite paleobiology. *Lethaia*, **28**: 333-353.
- JONES D.S., 1988. Sclerochronology and the size versus age problem. In MCKINNEY, M.L. (ed.) *Heterochrony in Evolution: a multidisciplinary approach*. New York, Plenum Press, 93-108.
- KUHL F.P. & GIARDINA C.R., 1982. Elliptic Fourier features of a closed contour. *Computer Graphic and Image Processing*, **18**: 236-258.
- LACROCE L. & REPETTO G., 2004. Validità specifica di *Trigonostoma parvotriangula* Sacco, 1894. *Bollettino Malacologico*, **40**: 15-24.
- LOMBARTE A., CHIC O., PARISI-BARADAD V., OLIVELLA R., PIERA J. & GARCÍA-LADONA E., 2006. A web-based environment for shape analysis of fish otoliths. The AFORO database. *Scientia Marina*, **70**: 147-152.
- READ D.W. & LESTREL P.E., 1986. Comment on uses of homologous point measures in systematics: a reply to Bookstein *et al.*, *Systematic zoology*, **35**: 241-253.
- TEMPLE J.T., 1992. The progress of quantitative methods in palaeontology. *Palaeontology*, **35**: 475-484.
- WATERS J.A., 1977. Quantification of shape by use of Fourier shape analysis: the Mississippian blastoid genus *Pentremites*. *Paleobiology*, **3**: 288-299.
- WHITE R.J., PRENTICE H.C. & VERWIJST T., 1988. Automated image acquisition and morphometric description. *Canadian Journal of Botany*, **66**: 450-459.